
THE IDENTITY OF *PAGURUS LEPIDUS* (BOUVIER) (DECAPODA, ANOMURA, PAGURIDAE) AND DESCRIPTION OF A NEW EASTERN PACIFIC INSULAR SPECIES

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ABSTRACT. The name *Pagurus lepidus* (Bouvier) has been assigned to several small closely allied hermit crab species in the Eastern Pacific. *Pagurus lepidus* is a member of the *provenzanoi* group of *Pagurus*, an informal group of the genus that has both Western Atlantic and Eastern Pacific representatives. Because species from the Pacific have not received the systematic attention afforded their Atlantic relatives, several species of the group from the Gulf of California, Mexico, western Central America, and Eastern Pacific atolls and archipelagos have been commonly referred to only as the *Pagurus lepidus* species complex.

Pagurus lepidus, herein redescribed and illustrated, is a geographically variable species, whose range is now documented from the Gulf of California, Mexico, to Peru. Certain specimens previously assigned questionably to *P. lepidus* are also described and illustrated as a new insular species, *P. nesiototes*, distributed from Clipperton Island to the Galapagos Archipelago.

INTRODUCTION

Pagurus lepidus (Bouvier) is one of the few named pagurids occurring in the shallow waters of the Gulf of California, Mexico, and as a result this name has been applied, at one time or another, to virtually all of the region's small hermit crabs with striped walking legs. Although it was Bouvier (1898) that first described *Pagurus lepidus* (as *Eupagurus*) from a collection made in the Gulf of California, the first documented capture of this species is from the Bay of Panama by J.G.H. Kinberg, zoologist aboard the Royal Swedish frigate "Eugenie", under the command of C.A. Virgin, during her circumnavigation of the world from 1851 to 1853. It remained, cataloged only as *Eupagurus* sp., in the collections of the Naturhistoriska Riksmuseet, Stockholm, until its recent rediscovery.

Some years ago one of us (JH) began to notice distinct, albeit subtle, differences in the color patterns among the Gulf of California pagurids. Sub-

sequent examinations revealed certain morphological differences as well. One character in particular, the lateral marginal plate of the telson, was found to differ among specimens. For example, in certain specimens the lateral margin was simply a weakly calcified or chitinous plate (Fig. 1A). In others this plate was terminated anteriorly by a prominent spine (Fig. 1B). In still others, this plate was composed of distinct individual spinules (Fig. 1C) or spines (Fig. 1D). These differences were found to correlate with some of the observed differences in color patterns.

Bouvier's description of *P. lepidus* was based on two specimens collected at "Baie de la Paz, Basse Californie", Mexico, and whereas his description was relatively detailed, it dealt with general characters and color patterns that have since proved to be analogous among several species. *Pagurus lepidus* is a moderately common intertidal to shallow subtidal species in the Gulf of California; however, it is not alone in exhibiting a preference for this habitat. Several additional, but undescribed, taxa have been confounded with this species (e.g., Haig *et al.*, 1970; Ball and Haig, 1974; Snyder-Conn, 1980). We have now had an opportunity to examine the syntypes of *Pagurus lepidus* and have found that only two of the subsequently published reports of this species (i.e., Glassell, 1937; Forest and de

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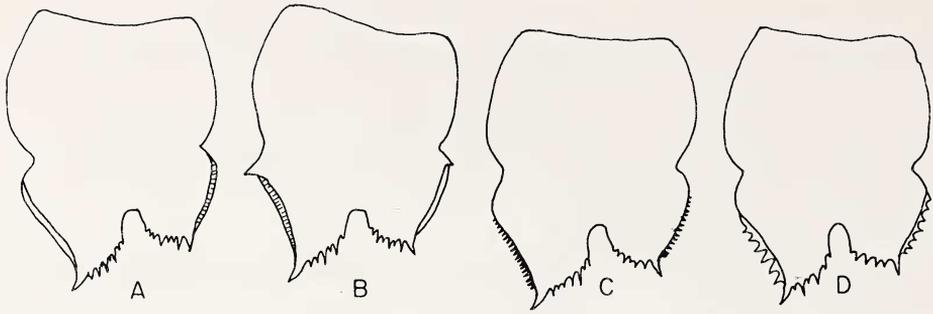


Figure 1. Diagrammatic telson types: A, simple entire or weakly marked lateral marginal plates on posterior lobes; B, entire or weakly marked lateral marginal plates of posterior lobes delineated by anterior spine(s); C, lateral marginal plates of posterior lobes divided into individual spinules; D, lateral marginal plates divided into prominent spines.

Saint Laurent, 1968) referred exclusively to this taxon. Specimens included in these other reports, as well as supplemental collections, represent new species that will be described in forthcoming publications.

Not only does *P. lepidus* exhibit the sexual dimorphism common to other members of the *provenzano* group of *Pagurus* (see McLaughlin, 1975), it has been found to also exhibit morphological variations correlated to its geographic distribution. Consequently, only a few characters and specific differences in color patterns can be used to separate *P. lepidus* from the other sympatric species of the subtropical and tropical Eastern Pacific. From the material available we have found that intraspecific variation in *P. lepidus* considerably exceeds that of most Western Atlantic species of the group as described by Lemaitre *et al.* (1982).

Chace (1962) reported *Pagurus lepidus* from Clipperton Island, noting that his specimens agreed in most characters with Bouvier's (1898) description but differed in the shape of the ocular acicles. We have reexamined the Clipperton Island specimens, and although clearly belonging to the *provenzano* group, they are distinct from all of the Gulf of California species of the *lepidus* complex and are herein described as *Pagurus nesiototes* new species.

MATERIALS

Materials for this study have come from the Crustacea collections formerly of the Allan Hancock Foundation (AHF) (now part of the Crustacea collection of the Natural History Museum of Los Angeles County), American Museum of Natural History (AMNH), Muséum National d'Histoire Naturelle, Paris (MNHN), National Museum of Natural History, Smithsonian Institution (USNM), Natural History Museum of Los Angeles County (LACM), Naturhistoriska Riksmuseet, Stockholm (NHRM), Smithsonian Oceanographic Sorting Center (SOSC), and from individual collectors. Specimens will be returned to their repositories of origin and/or deposited in these museums and the Rijksmuseum van Natuurlijke Historie, Leiden (RMNH). Material formerly belonging to the Allan

Hancock Foundation is indicated by an original AHF catalog number in addition to its current LACM number, which follows the AHF number in parentheses. One measurement, shield length (SL), provides an indication of size ranges of the specimens examined.

SYSTEMATICS

Pagurus lepidus (Bouvier, 1898)

Figures 2A–G, 3A–G

Eupagurus lepidus Bouvier, 1898:381.

Pagurus lepidus: Glassell, 1937:256; Chace, 1962:623 by implication (in part, see discussion); Forest and de Saint Laurent, 1968:116; Haig *et al.*, 1970:19 (in part, see discussion); Ball and Haig, 1974:102 (in part, see discussion); Snyder-Conn, 1980:283 (in part, see discussion).

Pagurus(?) *lepidus*: Moran, 1984:76, fig. 5.

?*Pagurus lepidus*: Von Prael, 1986:96 (see discussion).

Not ?*Pagurus lepidus*: Chace, 1962:623, fig. 2 (= *Pagurus nesiototes*, new species).

LECTOTYPE (herein selected). ♂ (SL 2.1 mm), MNHN, Paris, Pg 246, 1898. **Type locality.** Baie de la Paz, Basse Californie [Baja California Sur], Mexico.

PARALECTOTYPE. ♂ (SL = 2.2 mm), MNHN, Paris, Pg 246, 1898.

OTHER MATERIAL EXAMINED. Gulf of California, Sonora, Mexico: Puerto Peñasco, 1 ♂ (SL = 1.1 mm), November 23–26, 1955, collector E.P. Chace, USNM 99802; Puerto Peñasco, 1 ♂ (SL = 2.4 mm), intertidal, July 17, 1967, collector P. Pickens, AHF 2791-01 (LACM 67-241.1); Norse Beach, 3 ♂, 1 ovigerous ♀ (SL = 1.7–2.6 mm), Choya Bay Survey station 66033, shore, August 15, 1966, collectors T. & B. Burch, AHF 2789-01 (LACM 66-354.1); Norse Beach, 3 ♂, 2 ♀ (SL = 1.2–2.4 mm), shore, December 2, 1967, collector A. Havens, AHF 2790-01 (LACM 67-198.2); Coquina Reef, 1 ♂, 4 ovigerous ♀ (SL = 2.0–2.8 mm), lower intertidal, June 1973, collectors A. Kuris, M. Brody, E. Snyder, AHF 2792-01 (LACM 73-215.1); Station Beach, 3 ♂, 1 ♀, 2 ovigerous ♀ (SL = 2.0–2.4 mm), intertidal, July 27, 1988, collector A. Harvey, NHRM, RMNH D 38112; Station Beach, 9 ovigerous ♀ (SL = 1.4–2.1 mm), intertidal, December 1988, collector A. Harvey, USNM 244080; Turner's Island south of Tiburon Island, 3 ♂ (SL = 1.7–2.0 mm), "Velero III" station 1042-40, shore, January 24, 1940, AHF 2787-01 (LACM 40-14.5). Bahía La Paz, Baja California Sur, Mexico,

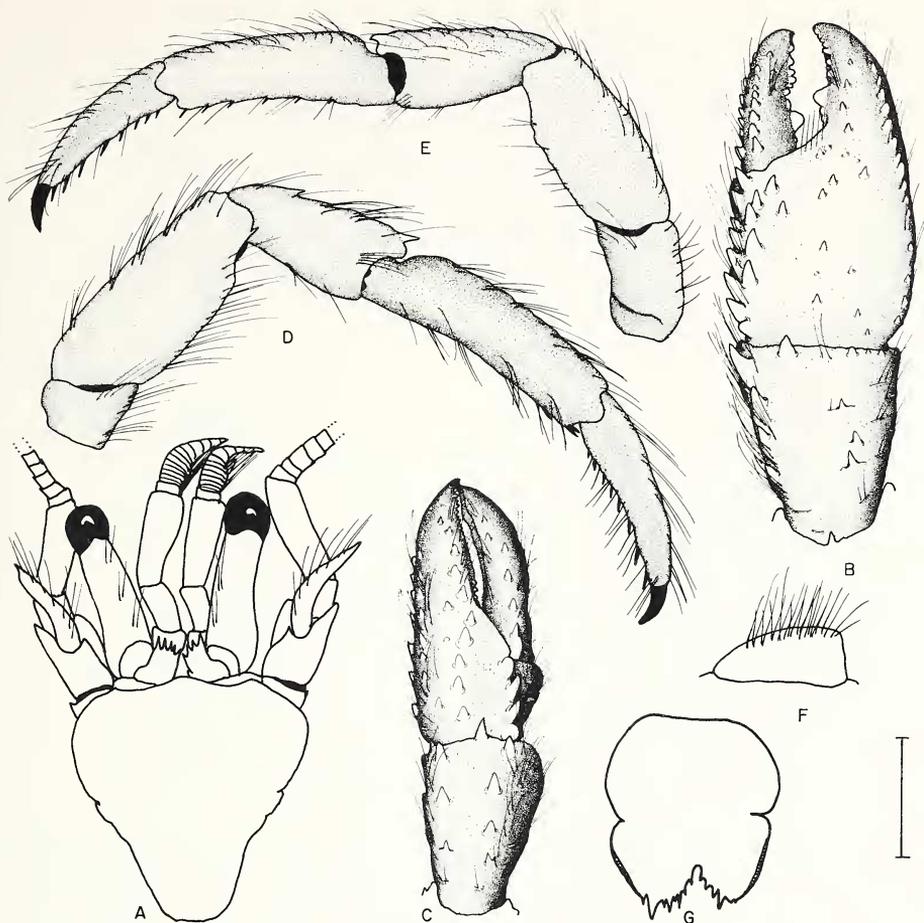


Figure 2. *Pagurus lepidus* (Bouvier) lectotype [MNHN Pg 24, Baja California Sur, Mexico]: A, shield and cephalic appendages; B, chela and carpus of right cheliped (dorsal view); C, chela and carpus of left cheliped (dorsal view); D, right 2nd pereopod (lateral view); E, left 3rd pereopod (lateral view); F, anterior lobe of sternite of 3rd pereopods; G, telson. Scale = 1 mm (A-E) and 0.5 mm (F, G).

26°50'45"N, 111°54'20"W, 3 ♂, 2 ovigerous ♀ (SL = 1.4–2.0 mm), Templeton Crocker Expedition "Zaca" station 144 D-1, 2 m, April 15, 1936, AMNH 12574. South Bay, Isla Cedros, W. Baja California Sur, Mexico, 1 ♀ (SL = 2.1 mm), "Velerio III" station 287-34, 20–30 m, March 10, 1934, AHF 2786-01 (LACM 34-161.3). Punta Pequeña, Bahía de San Juanico, W. Baja California Sur, Mexico, 2 ♂, 1 ♀ (SL = 1.6–2.7 mm), "Magbay" Expedition, 3.5 m, February 8, 1964, collectors T. Hopkins, T. Scanland, AHF 2788-01 (LACM 64-176.1). Outside Bahía Magdalena, W. Baja California Sur, Mexico, 1 ♂ (SL = 2.2 mm), "Magbay" Expedition, 20 m, February 1, 1964, collectors T. Hopkins, T. Scanland, AHF 2795-01 (LACM 64-177.1). Bahía Tenacatita, Jalisco, Mexico, 19°17'N, 104°50'W, 1 ♂ (SL = 1.7 mm), "Te Vega" Expedition station 18-22, 1.5–3.5 m, May 27, 1968, collector P. Smith, AHF 2629-03 (LACM 68-372.1). Mizata, Depto. La Libertad, El Salvador, 2 ♂ (SL = 1.5, 1.7 mm), shore, December 6, 1978, collector D. Moran, AHF 1623-01 (LACM 78-212.1). Gulf of Panama, 1 ♂ (SL = 1.5 mm), "Eugenie" Expedition, 1852, NHRM 7177. Panama Bay, Panama, 1 ♂, 1 ♀, 1 ovigerous ♀ (SL = 1.2–1.3 mm), December 12, 1981, collector T. Spight, AHF 2793-01 (LACM 81-129.1). Punta Paitilla, Panama, 8°58.1'N, 79°31'W, 1 ovigerous

♀ (SL = 1.5 mm), "Te Vega" Expedition station 18-14b, 2 m, May 6, 1968, collector E. Ball, AHF 2616-05 (LACM 68-373.1). Atacames Reef, Ecuador, 1 ♀ (SL = 1.2 mm), "Te Vega" Expedition station 18-8, 8 m, April 23, 1968, collectors M. Youngbluth, P. Smith, AHF 2607-03 (LACM 68-377.1). Manta, Ecuador, 0°56'S, 80°43'W, 1 ♂ (SL = 1.7 mm), "Te Vega" Expedition station 18-5, 6.3 m, April 19, 1968, collectors E. Ball, P. Smith, AHF 2605-06 (LACM 68-374.1). Punta Mandinga, Salinas, Ecuador, 2°11'S, 80°43'W, 2 ♂, 2 ovigerous ♀ (SL = 0.8–1.4 mm), "Te Vega" Expedition station 18-4, intertidal, April 16, 1968, collector E. Ball, AHF 2604-03 (LACM 68-376.1). Talara, Peru, 4°34'S, 81°07'W, 4 ♂, 4 ovigerous ♀ (SL = 1.3–1.8 mm), "Te Vega" Expedition station 18-2, 5 m, April 9, 1968, collector E. Ball, AHF 2602-02 (LACM 68-375.1).

DIAGNOSIS. Shield longer than broad. Ocular acicles multispinose. Antennal flagellum with 1–3 short setae each article and scattered longer setae. Carpus of right cheliped with 4 or 5 spines on dorsomesial margin. Left cheliped with dorsomesial surface of palm horizontal, margin with row of protuberances or spines. Dactyli of ambulatory legs

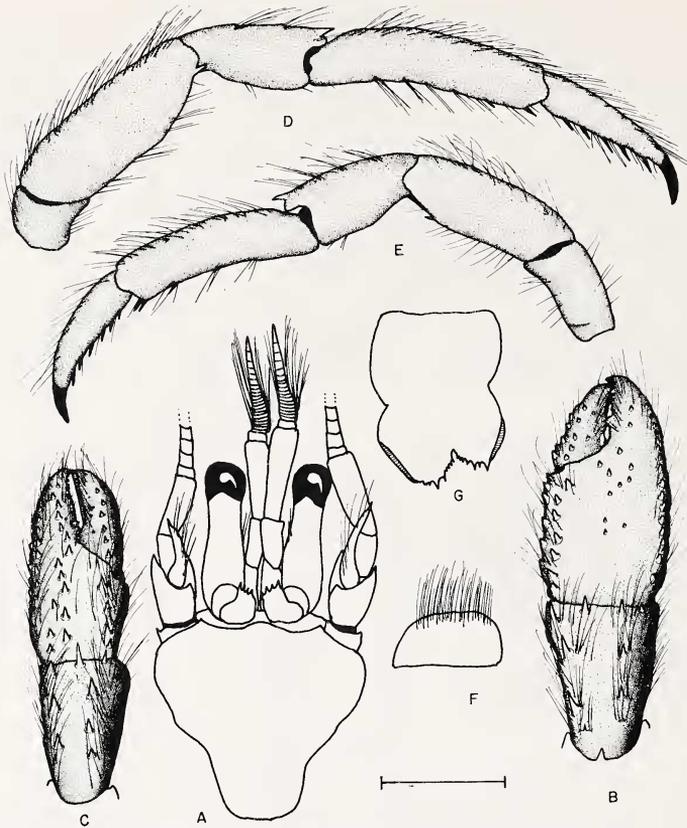


Figure 3. *Pagurus lepidus* (Bouvier) [NHHRM 7177, Bay of Panama]: A, shield and cephalic appendages; B, chela and carpus of right cheliped (dorsal view); C, chela and carpus of left cheliped (dorsal view); D, right 2nd pereopod (lateral view); E, left 3rd pereopod (lateral view); F, anterior lobe of sternite of 3rd pereopods; G, telson. Scale = 1 mm (A-E) and 0.5 mm (F, G).

each with 5-9 corneous spines on ventral margin; carpi each with spine at dorsodistal margin and P_2 also with dorsal surface usually slightly spinulose or with 1 small spine proximally. Posterior lobes of telson with terminal margins oblique, lateral margins with narrow, undifferentiated plate and without delimiting spine anteriorly. In life, chelipeds with distal four-fifths of fingers greenish-white or white; meri with pinkish-white band distally. Ambulatory legs with greenish-brown longitudinal stripes.

REDESCRIPTION. Shield longer than broad, anterior margin between rostrum and lateral projections concave, posterior margin roundly truncate. Rostrum obsolete, unarmed; lateral projections unarmed or with minute terminal spinule. Dorsal surface of shield with scattered tufts of setae.

Ocular peduncles one-half to four-fifths length of shield, broadened basally and with corneae slightly dilated, with longitudinal row of tufts of setae on dorsomesial face. Ocular acicles somewhat subquadrate, with 3-6 terminal marginal spines; separated basally by approximately one-half basal width of 1 acicle.

Antennular peduncles overreaching ocular peduncles by one-fourth to one-half length of ultimate segment. Ultimate segment with scattered setae dorsally and ventrally. Penultimate segment with few setae ventrally. Basal segment with 1 acute spine on dorsolateral face.

Antennal peduncles slightly overreaching corneae. Fifth and 4th segments with few tufts of setae. Third segment unarmed or with very small spinule at ventrodistal margin. Second segment with dorsolateral distal angle produced, terminating in acute spine, lateral and mesial margins occasionally with accessory small spine and with long or moderately long setae; dorsomesial distal angle unarmed or with small spine, mesial face with long setae. First segment with small spine on lateral face distally, particularly apparent in small individuals, ventral margin produced and armed with 1 spine laterally. Antennal acicle somewhat arcuate, terminating in small spine, mesial margin with moderately long setae. Antennal flagellum with 1-3 short setae or bristles on every article and frequently also with scattered longer setae (1-2 articles in length).

Right cheliped with dactylus equal to or as much as one-half again as long as palm. Slight hiatus be-

tween dactylus and fixed finger. Cutting edge of dactylus varying from 1 strong calcareous tooth in proximal half and small calcareous teeth distally to 1–3 small calcareous teeth proximally and row of corneous teeth distally, terminating in corneous tip. Cutting edge of fixed finger with 1 strong and several small calcareous teeth in proximal half and row of small corneous teeth interspersed with small calcareous teeth in distal half or only with alternating calcareous and corneous teeth, terminating in small calcareous or corneous claw. Dactylus overlapped by fixed finger. Dorsomesial margin of dactylus with row of small acute spines and long setae, dorsal surface slightly elevated in midline and also armed with row of small spines and tufts of long stiff setae, ventral surface with tufts of long stiff setae. Palm one-half to two-thirds length of carpus; dorsomesial margin with irregularly double row of spines, strongest proximally, dorsal surface with numerous tufts of long stiff setae and varying in armature from scattered spinules or small spines and median inverted V-shaped row of stronger spines to only few scattered spinules, dorsolateral margin with low protuberances proximally becoming row of small spines on fixed finger or row of spines increasing in size on fixed finger. Fixed finger often with irregular row of small spines. Carpus slightly shorter to slightly longer than merus; dorsomesial margin with row of 4 or 5 rather widely spaced spines, 1 or 2 spines on or near distal margin, dorsal surface unarmed or slightly spinulose and with tufts of long setae, dorsolateral margin unarmed or with row of spines, distolateral margin sometimes with small spine and ventrolateral distal angle usually with acute spine, lateral and mesial faces with scattered setae. Merus subtriangular; dorsal margin with few tufts of setae and often small spine on distal margin, ventromesial and ventrolateral margins unarmed or with 1 small spine on ventromesial margin and short row of small spines on ventrolateral margin in distal half. Ischium unarmed.

Left cheliped with dactylus and fixed finger somewhat spoon-shaped. Cutting edge of dactylus with row of corneous teeth, terminating in corneous claw; dorsal surface with row of stiff setae near cutting edge, midline with row of spines and frequently 2nd row of longer setae, dorsomesial margin with low protuberances or row of small spines; mesial margin and ventral surface also with tufts of long setae. Palm one-half to two-thirds length of carpus; midline armed with irregular double row of spines, extending onto the fixed finger as single row adjacent to cutting edge, dorsolateral face strongly sloping ventrally, with row of tufts of long setae and usually row of small spines in ventral half and 2nd row of protuberances or spines and tufts of long setae marginally, dorsomesial face horizontal with margin marked by row of protuberances or moderate to strong spines and tufts of setae, mesial face with low protuberances and tufts of setae. Carpus usually equaling merus in length; dorsomesial and dorsolateral margins each with row of strong

spines and tufts of long setae, dorsodistal margin with 1 strong spine, dorsal surface and mesial and lateral faces with scattered setae. Merus triangular; dorsal margin with tufts of setae, ventrolateral margin with row of acute spines in distal half, ventromesial margin with row of spines, usually only on proximal half in large males, ventral surface with long setae laterally. Ischium with acute spine at ventrolateral distal angle and often also with row of small spines on ventromesial margin.

Second and 3rd pereopods with dactyli and propodi varying in length and width; 3rd right usually longest and most slender, 3rd left shortest and broadest. Dactyli slightly less than half to almost equaling length of propodi, approximately one-third to one-fifth as broad (proximally) as long, terminating in strong curved corneous claws; dorsal, mesial, and lateral surfaces all with tufts of moderate to long setae, ventral margins each with row of 5–9 corneous spines and long stiff setae. Propodi exceeding length of carpi by one-fourth to one-third own length; dorsal surfaces with tufts of long stiff setae, ventral surfaces each with pair of corneous spines at distal margin and 1 additional spine in distal third (2nd) or 1st, 2nd, or 1st and 2nd paired spines followed by row of widely spaced corneous spines proximally (3rd). Carpi approximately equaling length of meri; dorsodistal margins each with 1 small spine, dorsal surfaces with low protuberances, 2nd usually slightly spinulose and/or with small spine developed proximally, also with tufts of long setae, mesial and lateral faces and ventral surface with scattered setae. Meri with tufts of long setae on dorsal margins; ventral margins with low protuberances and tufts of long setae or with small spine on ventrolateral margin distally (2nd). Ischia with row of long setae on ventral margins.

Anterior lobe of sternite of 3rd pereopods subrectangular to subsemicircular, unarmed. Fourth pereopods with small preungual process at base of claw; propodal rasp with 5–8 rows of corneous scales; dorsal margins of dactyli, propodi, carpi, and meri (distally) with very long dense setae.

Exopod of left uropod with row of 6–10 thick setae on inner margin. Telson with terminal margins oblique, each armed with row of spines, 1 or 2 usually stronger and sometimes corneous-tipped; lateral margins delimited by narrow plate, no anterior spine.

COLOR. Northern Populations in Life. Antennal flagellum with 2 transparent articles proximally followed by greenish-brown articles interrupted every 3 articles by 1 white or transparent article. Shield transparent centrally with mottled green flecked with yellow marginally and posteriorly. Ocular peduncles mottled greenish-brown on white with flecks of pink distally and dorsal patch of pink proximally, corneae crimson; acicles with reddish-brown flecks on greenish-white background, distal margin without flecks. Antennular peduncles with ultimate and penultimate segments greenish-white with red flecks, basal segment greenish-white in distal half and pink

in proximal half. Chelipeds greenish-brown or olive with white spines often tinged with dark red-brown basally on palms and carpi, distal four-fifths of fingers white or greenish-white, meri with distal pinkish-white band and remainder mottled greenish or olive flecked with reddish-brown. Ambulatory legs with dactyli greenish-white distally and greenish-brown with short darker greenish-brown longitudinal stripes proximally; propodi with pink patch on lateral face near distal margin and pink band proximally, greenish-brown longitudinal stripes on greenish or grayish-white background centrally; carpi with light pink distally and dark greenish-brown longitudinal stripes on greenish or grayish-white background in proximal two-thirds; meri pink proximally and distally with dark greenish-brown longitudinal stripes on light green or gray background centrally (PAMcL, unpublished data).

Southern Population in Life. Antennal flagellum usually with 3 olive drab articles interrupted by 1 white article. Shield mottled olive drab and white. Ocular peduncles mottled white and olive drab, corneae red. Antennular peduncles with white patch dorsally and green bands proximally on ultimate segment and dark green band distally on penultimate segment. Chelipeds with white dactyli, and fixed fingers, palms, carpi, and meri mottled olive drab and white. Ambulatory legs with distal halves of dactyli white, proximal halves with short brown stripes; propodi with longitudinal brown stripes on pale background, with yellow spots between stripes; carpi and meri with dark brown longitudinal stripes on pale background (E.E. Ball, field notes).

In Preservative. Palms and carpi of chelipeds reddish-orange, fingers white. Stripes of ambulatory legs reddish-orange. All color fading with time to straw yellow.

DISTRIBUTION. West Pacific coastal Baja California, Baja California Sur, and Gulf of California, Mexico to Peru; intertidal to 20 m.

AFFINITIES. As previously indicated, *Pagurus lepidus* is the name that has been applied to at least six small hermit species occurring in the shallow waters of the Eastern Pacific. All of these species are similar in morphology and color patterns. Distinctions among the species can only be made by careful structural examination or comparisons of colors in living animals. These structural characters include the multispinose condition of the ocular acicles, as opposed to the simple, single-spined condition; the presence of short setae on the articles of the antennal flagellum rather than long (more than three articles in length), randomly placed or serially paired setae; and the horizontal as opposed to sloping dorsomesial face of the left chela. Although *P. lepidus* exhibits considerable variations over its geographic range, it can be distinguished from the majority of similarly striped species by the absence of an anterior spine on the lateral margin of the posterior telsonal margin plates and by the almost horizontal dorsomesial surface of the left chela. The setation of the antennal flagellum, con-

sisting of short and scattered moderately long (one to two articles in length) in *P. lepidus* is diagnostic only when compared with species having truly long and/or serially paired setae.

VARIATIONS. There are distinct differences between the specimens of *P. lepidus* collected in the Gulf of California and the outer coast of the Baja California Peninsula and those from Central and South America. If specimens from the extremes of the range are examined, these differences appear significant enough to suggest that two distinct taxa may be involved. However, despite the relative paucity of material from the central portion of the range (southern Mexico and northern Central America), we have observed enough character clines to convince us that we are dealing with one highly variable species.

The Puerto Peñasco, Sonora, Mexico, region was the source of more than half of the specimens examined. A characteristic of *P. lepidus* from this region is a difference in the length-width ratios of the dactyli of the left and right 3rd pereopods, regardless of overall body size. Proximally the 3rd left dactylus is one-third to one-fourth as broad as long, whereas the 3rd right is usually only one-fourth to one-fifth as broad as long. At this apparent northern end of its range, *P. lepidus* reaches a large overall size (shield length in excess of 2.5 mm), and with increasing size additional morphological changes in the ambulatory legs usually occur that have not often been observed in the Central and South American population. This is particularly apparent in the length relationships of the dactyli to their respective propodi. In small individuals (shield lengths less than 1.7 mm) within this northern population, the dactyli, especially the 3rd left, usually are from three-fourths to nine-tenths the length of the propodi; both segments are visually quite short. With increasing size, the dactyli become more slender and the propodi elongate. In specimens with shield lengths greater than 2.0 mm, the length of the dactylus varies from two-thirds to sometimes less than one-half the length of the propodus. Concurrent with changes in dactylar length and width are changes in the armature of the ventral margins. Small specimens commonly have six or seven corneous spines on the ventral margins of the dactylus. With increasing size, the number of spines increases to seven to nine or occasionally 10. Generally the armature of the right chela consists of scattered moderately strong spines on the dorsal surface of the palm, with an inverted V of stronger spines medianly. However, with increasing size, the strength of the chela armature is reduced, becoming virtually obsolete in very large specimens. Frequently the ischium of the left cheliped is armed with a row of small spines.

None of the specimens collected in the southern half of the range of *P. lepidus* had a shield length in excess of 2.0 mm, and this may be the reason that no marked changes in length-width ratios in the dactyli of the right and left 3rd pereopods were

observed. The length relationships between propodi and dactyli, however, were different in this smaller southern population. Generally the dactyli were two-thirds to three-fourths as long as the propodi. Similarly, the number of spines on the ventral margins of the dactyli varied from five to six. Few specimens exhibited strong spination on the dorsal surface of the right chela, and no spines were observed on the ventral margin of the ischium of the left chela. In the color descriptions reported for the two populations, slight variations also could be detected.

However, there are exceptions. For example, the only notable difference between the lectotype (Fig. 2A-G) and the Panamanian specimen collected by the "Eugenie" (Fig. 3A-G) is the number of dactylar spines on the ventral margins of the 2nd and 3rd pereopods. Among the northern populations a few specimens of comparable size to those found farther south, including one specimen from Puerto Peñasco, had proportionally longer dactyli and only five spines on the ventral margins. Similarly, one of the southern specimens had an appreciably more slender 3rd right dactylus with seven spines on the ventral margin. Geographically correlated differences were apparent among the 58 specimens we critically examined, but there was a sufficient number of intermediate conditions to suggest a clinal variation from north to south.

DISCUSSION. Bouvier's (1898) description included many of the general characteristics of most species assignable to the "*Pagurus lepidus*" complex, e.g., obtusely rounded rostrum, multispinose ocular acicles, spinulose chelipeds, striped ambulatory legs. Bouvier was not aware of the number of distinct taxa in the region that could be described by these same characters.

Glassell (1937) did not provide a description of his specimens other than certain characters cited in his key to distinguish this taxon from other *Pagurus* species collected by the Templeton Crocker Expedition. None of these characters will separate *P. lepidus* from the other Eastern Pacific species of the complex. Although Glassell did describe color patterns remaining in his preserved material, these patterns fit at least three species of the complex. We have been able to reexamine these specimens now housed in the collection of the American Museum of Natural History and can confirm their identity as *P. lepidus*.

In his questioned referral of the Clipperton Island specimens to *P. lepidus*, Chace (1962) used for comparison a lot of specimens in the national collections that had previously been identified as *P. lepidus*. We have reexamined this lot from Puerto Peñasco, Mexico (USNM 99802), and found that only one of the eight specimens actually is *P. lepidus*. The remaining seven specimens represent an undescribed species (Harvey and McLaughlin, 1990). Chace (1962) recognized that his Clipperton Island specimens possessed ocular acicles with a single terminal spine, whereas the ocular acicles of Bou-

vier's (1898) *P. lepidus* and the Puerto Peñasco specimens had multispinose acicles. Although he was unwilling to designate a new species on the basis of one lot of comparative material, he suspected that the Clipperton Island specimens might, in fact, represent a distinct taxon. We have now been able to confirm that suspicion.

Haig *et al.* (1970) and Ball and Haig (1974) recognized that several species were probably confounded under the name *P. lepidus*. However, as they did not have access to Bouvier's (1898) material at that time, they were unable to accurately distinguish among these taxa. We have reexamined the materials included in both of these reports and have found that one lot of specimens from Punta Pequeña, Bahía de San Juanico, Baja California Sur, Mexico (Haig *et al.*, 1970), and specimens from Mexico, Ecuador, and Peru (Ball and Haig, 1974) do represent *P. lepidus*.

Snyder-Conn (1980) gave a generalized description of *P. lepidus* but repeated Haig's opinion that this species had been confounded with several others represented in the Gulf of California fauna. Although one specimen that she collected has proved to be *P. lepidus*, it is probable that she included other local taxa in her report.

Moran (1984) provided notes and illustrations of the hermit crabs he identified as *Pagurus* (?) *lepidus*. However, he remarked that his identification was doubtful because this was one of several closely related species of the genus that were in need of revision. We have been able to examine two of his five specimens. These, at least, do represent *P. lepidus*.

Pagurus lepidus was among the decapods listed by Von Prah (1986) as inhabiting a coral rubble community in Utria Sound, Colombia. *Pagurus lepidus* is known from this type of habitat, and the locality is within its distributional range. However, Von Prah's report can only questionably be included in the synonymy of *P. lepidus* as other *provenzanoi* group species have similar habitats and ranges. Von Prah was unfortunately killed in a plane crash in 1989, thus his material has not been available for verification.

More recently five other references to "*Pagurus lepidus*" have come to our attention, i.e., Westervelt (1967), Romero (1982), Rodriguez de la Cruz (1987), Romero and Carvacho (1988), and Villalobos Hiriart *et al.* (1989). None have been cited in the synonymy of this species as it is impossible to know which, or how many, of the species heretofore confounded under the name *P. lepidus* may be represented by these reports.

***Pagurus nesiotetes* new species**

Figures 4A-G, 5A-F

?*Pagurus lepidus*: Chace, 1962:623, fig. 2. Not *Pagurus lepidus* (Bouvier).

Pagurus sp.: Birkeland *et al.*, 1975:67.

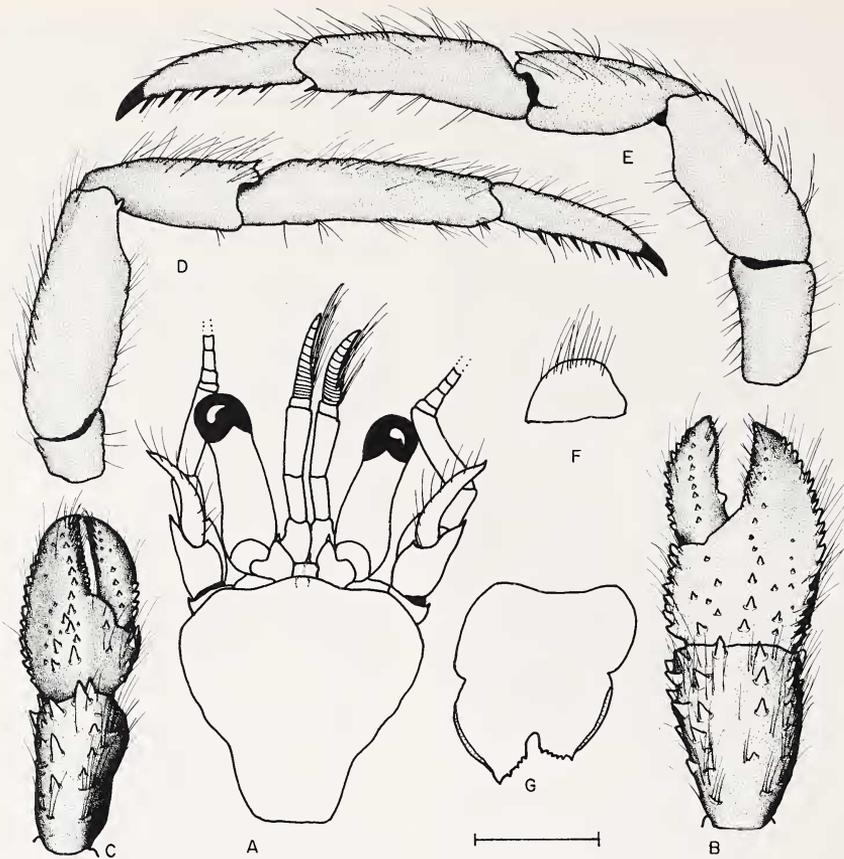


Figure 4. *Pagurus nesiotes* new species, paratype [USNM 22194, Clipperton Island]: A, shield and cephalic appendages; B, chela and carpus of right cheliped (dorsal view); C, chela and carpus of left cheliped (dorsal view); D, right 2nd pereopod (lateral view); E, left 3rd pereopod (lateral view); F, anterior lobe of sternite of 3rd pereopods; G, telson. Scale = 1 mm (A-E) and 0.5 mm (F, G).

HOLOTYPE. Ovigerous ♀ (SL = 2.0 mm). **Type locality.** Clipperton Island, NE side, 15 m, August 28, 1958, collectors [Limbaugh, Chess, Hambly], USNM 110975.

PARATYPES. 1 ♂, 1 ovigerous ♀ (SL = 1.8, 1.4 mm). Clipperton Island, NE side, 15 m, August 28, 1958, collectors [Limbaugh, Chess, Hambly], USNM 221940. Malpelo Island, Colombia, 3 ♂ (SL = 1.6–1.8 mm), subtidal, February 29–March 3, 1972, collector C. Birkeland, AHF 728 (LACM 72-345.1). Galapagos Islands: Charles Island, 1 ♀ (SL = 1.5 mm), “Eugenie” Expedition, 15–22 m, May 15–17, 1852, NHRM 7167; Post Office Bay, Charles Island, 1 ♂ (SL = 1.3 mm), “Velero III” station 167-34, 30 m, January 19, 1934, AHF 3424 (LACM 34-40.4); Post Office Bay, Charles Island, 3 ♂ (SL = 1.2–1.6 mm), “Velero III” station 193-34, 15–18 m, January 27, 1934, AHF 3426 (LACM 34-67.4); off James Bay, James Island, 1 ♂ (SL = 1.4 mm), “Velero III” station 182-34, 60 m, January 24, 1934, AHF 3425 (LACM 34-56.2); west side Academy Bay, Santa Cruz Island, 3 ♂, 1 ♀, 1 ovigerous ♀ (SL = 1.3–2.4 mm), 3–8.5 m, August 25–27, 1976, collector P. Abrams, formerly AHF 762, now divided between MNHN, RMNH D 38105; 00°54′11″S, 90°18′15″W, 12 ♀, 3 ovigerous ♀, 5 juveniles (SL = 0.6–2.2 mm), “Anton Bruun” station 16/66112, 8–10 m, May 19, 1966, collector S. Earle, SOS; south end of Darwin (Culpepper)

Island, 2 ♂, 2 ♀ (SL = 1.2–2.2 mm), approximately 11 m, May 13, 1984, LACM 84-29.4; south side of Darwin (Culpepper) Island, 2 ♂ (SL = 1.3, 2.3 mm), 9–13 m, May 13, 1984, LACM 84-29.5; northwest side of Pinta (Abingdon) Island, 1 ♂, 1 ovigerous ♀ (SL = 1.8, 2.0 mm), 10–13 m, May 17, 1984, LACM 84-37.1; off Punta Espejo, east end Marchena (Bindloe) Island, 1 ovigerous ♀ (SL = 1.9 mm), 12 m, May 11, 1984, LACM 84-26.1.

DIAGNOSIS. Shield as long or longer than broad. Ocular acicles terminating in single spine. Antennal flagellum naked or with 1–4 very short setae every 1–4 articles. Carpus of right cheliped with irregular double row of spines on dorsomesial margin. Left cheliped with dorsomesial surface of palm strongly sloping, margin usually spinulose or spinose. Dactyli of ambulatory legs with 6–10 corneous spines on ventral margins; carpi each usually with spine at dorsodistal margin. Posterior lobes of telson with terminal margins oblique to rounded, lateral margins with narrow plate undifferentiated or with individual denticles clearly distinguishable, no delimiting spine anteriorly. In preservative, chelipeds with finger tips white, carpal and meral segment solidly

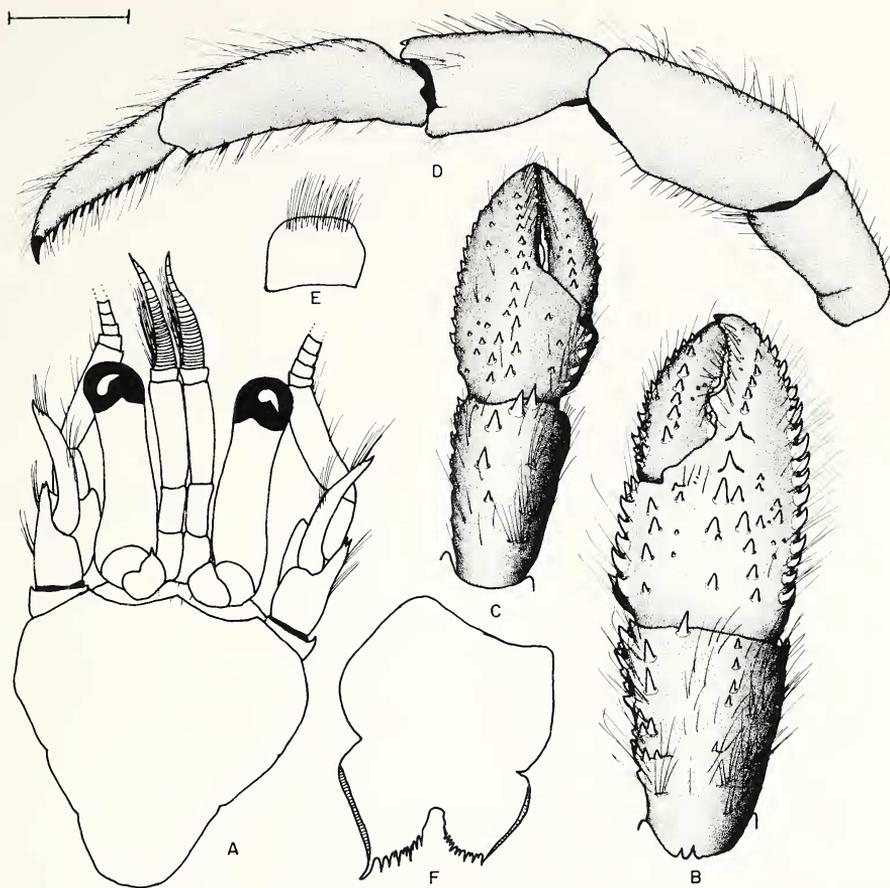


Figure 5. *Pagurus nesiotes* new species, paratype [formerly AHF 762; now RMNH D 38105; Galapagos Islands]: A, shield and cephalic appendages; B, chela and carpus of right cheliped (dorsal view); C, chela and carpus of left cheliped (dorsal view); D, left 3rd pereopod (lateral view); E, anterior lobe of sternite of 3rd pereopods; F, telson. Scale = 1 mm (A-E) and 0.5 mm (F).

colored. Ambulatory legs each with longitudinal stripes and additional broad distal band on merus.

DESCRIPTION. Shield equal to or longer than broad, anterior margin between rostrum and lateral projections concave, anterolateral margins sloping or slightly terraced, posterior margin roundly truncate. Rostrum obsolete or obtusely triangular, sometimes weakly produced; lateral projections broadly rounded or obtusely triangular, unarmed. Dorsal surface of shield with scattered setae.

Ocular peduncles one-half to four-fifths shield length, broad basally, and usually tapering to very slightly dilated corneae. Ocular acicles subtriangular to subovate, terminating in 1 marginal or submarginal spine, rarely with 2nd spine in close proximity; separated basally by two-thirds basal to slightly more than basal width of 1 acicle; interocular lobes weakly developed.

Antennular peduncles equaling or exceeding ocular peduncles by up to one-half length of ultimate segment. Ultimate segment with few setae on dorsal surface. Penultimate segment with few scattered

setae. Basal segment with 1 acute spine on dorso-lateral margin.

Antennal peduncles overreaching corneae by less than one-fourth to more than one-third length of ultimate segment. Fifth and 4th segments with few tufts of setae. Third segment with acute spine at ventrodistal margin, partially obscured by tuft of setae. Second segment with dorsolateral distal angle produced, terminating in 1 or 2 spines, lateral margin sometimes with small spine distally and with long setae; dorsomesial distal angle unarmed or with small spine, mesial face with scattered setae. First segment with small spine on lateral face distally, ventral margin produced and armed with 1 spine laterally. Antennal acicle somewhat arcuate, terminating in usually acute spine, mesial margin with moderately long setae. Antennal flagellum naked or with 1-4 very short setae every 1-4 articles.

Right cheliped with dactylus one-fourth to one-half again as long as palm. Slight hiatus between dactylus and fixed finger. Cutting edge of dactylus with 1 strong and several small calcareous teeth in

proximal half and row of very small calcareous teeth distally, terminating in small corneous claw. Cutting edge of fixed finger with 1 very prominent broad tooth proximally and small calcareous teeth distally, terminating in corneous tip. Dactylus equaling or exceeding length of propodus by approximately one-fourth own length with single or double row of small acute spines on dorsomesial margin proximally but sloping ventrally to tip, dorsal surface somewhat elevated in midline and armed with row of strong spines and long setae, mesial and ventral surfaces with scattered long setae. Palm equaling or two-thirds the length of carpus; dorsomesial margin with irregular row of acute strong spines and often 2nd adjacent row, dorsal surface with scattered small spines, 2 rows of strong spines occasionally forming inverted V in midline and extending onto fixed finger as row of smaller spines, dorsolateral margin with row of moderately weak to strong spines, decreasing in size on fixed finger, surfaces with scattered long setae. Carpus equaling or slightly longer than merus; dorsomesial margin with double, sometimes irregular, row of spines, 1 or 2 spines on or near distal margin, dorsal surface with row of smaller spines laterad of midline, tending to become obsolete in large individuals, dorsolateral margin not delimited or with row of small spines, lateral face with tufts of long setae, laterodistal margin often with 1 or 2 spines dorsally, ventrolateral margin usually with 1 or 2 spines distally, mesial face with scattered setae. Merus subtriangular; dorsal margin with tufts of setae, distal margin with 1 or 2 spines, ventromesial and ventrolateral margins each with row of spines, strongest laterally. Ischium unarmed or with row of small spines or low tubercles on ventromesial margin.

Left cheliped with dactylus and fixed finger somewhat spoon-shaped. Dactylus one and one-fourth to twice length of palm; cutting edge with row of corneous teeth, terminating in corneous claw. Cutting edge of fixed finger with small calcareous teeth that may be replaced distally with corneous teeth. Dorsal surface of dactylus with row of small spines in proximal half near cutting edge and row of spines or spinulose tubercles on dorsomesial margin, surfaces with scattered long setae. Palm one-third to one-half length of carpus; dorsal surface with midline elevated and armed with irregular double row of strong spines, extending onto fixed finger as single row, dorsomesial face strongly sloping ventrally, armed with irregular row of very small spines or spinules in ventral half and single or double row of spines marginally, dorsomesial face strongly sloping, surface and margin each sometimes with row of moderate to strong spines or only with few small spinules, all surfaces with scattered long setae. Carpus equaling or slightly shorter than merus; dorsolateral margin with row of strong spines and tufts of long setae, dorsomesial margin with few spines or more frequently with few spinulose tubercles, distal margin usually with strong spine, lateral face sometimes spinulose, laterodistal margin usually

with 2 or 3 spines, ventrolateral margin with row of strong acute spines, mesial face with scattered setae and occasionally 1 or 2 small spinules or tubercles on ventromesial margin distally. Merus triangular; dorsal margin with tufts of setae, ventromesial margin with 2 to several spines, ventrolateral margin with row of acute spines and long setae. Ischium with acute spine at ventrolateral distal angle and usually with row of small spines on ventromesial margin.

Second and 3rd pereopods similar. Dactyli one-half to two-thirds length of propodi (shortest on left 3rd and generally shorter in larger individuals), one-third to one-sixth as broad proximally as long, terminating in strong curved corneous claws, dorsal, mesial, and lateral faces all with scattered moderate to long setae, ventral margins each with row of 6–10 corneous spines and few short to moderately long setae. Propodi exceeding length of carpi by one-fourth to one-third own length; dorsal surfaces with tufts of long setae; ventral surfaces each with corneous spine at distal margin (2nd) and often 1 or 2 additional spines in distal third or occasionally row of spinules (3rd). Carpi one-half to three-fourths length of meri; dorsodistal margins each usually with 1 small spine, occasionally lacking on left 3rd, dorsal surfaces with low protuberances and tufts of long setae, mesial and lateral faces and ventral surface with scattered setae. Meri each with low protuberances on dorsal and ventral surfaces, lateral face of 2nd with strong acute spine at ventrodistal angle and sometimes with 1 or 2 spines on ventral margin (left). Ischia with few setae on dorsal and ventral margins.

Anterior lobe of sternite of 3rd pereopods varying from subrectangular to subsemiovalate, unarmed. Fourth pereopods apparently without preungual process at base of claw; propodal rasp of 4 or 5 rows of corneous scales; dorsal margins of segments with long setae.

Exopod of left uropod with row of 3–6 thick setae and frequently 1 or 2 thinner setae on inner margin. Telson with posterior lobes subtriangular; terminal margins oblique or rounded, each armed with row of spines, largest at external angle; lateral margin with narrow plate delimited, sometimes with individual denticles clearly developed; no anterior spine.

COLOR (in formalin for 2 months). Shield and ocular acicles pale orange. Antennular peduncles purple, penultimate segment with distal orange ring; flagellum orange. Antennal peduncles orange, distal segment with longitudinal red stripe; acicle orange with white tip. Ocular peduncles pale with random purple blotches. Chelipeds orange with purple tubercles; chelae paler, with white fingers; meral and carpal segments red. Meri of 2nd and 3rd pereopods purple with broad distal orange band; carpi purple with little orange distally; proximal halves of propodi purple, distal halves white with patch of orange distally; dactyli white with purple proximally. All areas appearing purple overlaid with nar-

row longitudinal stripes. Fourth and 5th pereopods pale orange (JH, unpublished data, lab notes).

DISTRIBUTION. Clipperton Island, Malpelo Island, and Galapagos Archipelago; subtidal to 60 m.

ETYMOLOGY. The specific name is from the Greek *nesiotes*, an island dweller; a noun in apposition.

AFFINITIES. Of species within the *P. lepidus* complex, *P. nesiotes* appears most closely related to *Pagurus villosus* Nicolet, 1849, with which it shares the less common character, simple ocular acicles. *Pagurus nesiotes* can immediately be distinguished from *P. villosus* by the setation of the antennal flagella. In the former species one to four short setae are present on every one to four articles. In the latter species a pair of long setae is present on each article, at least in the proximal half. *Pagurus nesiotes* is distinguishable from *P. lepidus* not only by its simpler ocular acicles but by the marked slope of the dorsomesial face of its left chela.

DISCUSSION. As previously indicated, Chace (1962) believed that his Clipperton Island specimens agreed in most general respects with Bouvier's (1898) description of *P. lepidus* and with specimens from Puerto Peñasco, Sonora, Mexico, previously identified as *P. lepidus*. However, he noted one striking difference, i.e., the lack of multispinose ocular acicles, which were described for *P. lepidus* and which were present in the Mexican specimens. Although Chace (1962) felt that it was quite possible this character might prove to be of specific importance, he was reluctant to assign a new specific name to the Clipperton Island material until more information was available from other localities.

We have been able to examine the specimen discussed in Birkeland *et al.* (1976) and cited in that report only as *Pagurus* sp. It too is *P. nesiotes*. As far as is presently known, this is truly an insular species.

ACKNOWLEDGMENTS

We are indebted to Harold Feinberg, American Museum of Natural History, Jacques Forest, Muséum National d'Histoire Naturelle, Paris, Raymond Manning, National Museum of Natural History, Smithsonian Institution, and Rafael Lemaitre, Smithsonian Oceanographic Sorting Center, for making their specimens of *P. lepidus* and *P. nesiotes* available to us. One of us (PAMcL) also thanks the Swedish National Science Research Council and Drs. Å. Franzen and Å. Andersson of the Invertebrate Section of the Naturhistoriska Riksmuseet, Stockholm, for providing the opportunity to work with the Museum's pagurid collections. We acknowledge, with thanks, the several collectors who have deposited their collections with the Allan Hancock Foundation or provided material for this study: P. Abrams, E. Ball, T. and B. Burch, D. Moran, A. Harvey, A. Havens, T. Hopkins, A. Kuris, P. Pickens, T. Scanland, J. Stames, and T. Spight.

LITERATURE CITED

- Ball, E.E., and J. Haig. 1974. Hermit crabs from the tropical eastern Pacific. I. Distribution, color, and natural history of some common shallow-water species. Bulletin of the Southern California Academy of Sciences 73:95-144.
- Birkeland, C., D.L. Meyer, J.P. Stames, and C.L. Buford. 1976. Subtidal communities of Malpelo Island. In *The biological investigation of Malpelo Island, Colombia*, ed. J.B. Graham, 55-68. Smithsonian Contributions to Zoology no. 176.
- Bouvier, E.L. 1898. Sur quelques Crustacés anomoures et brachyures recueillis par M. Diguët en Basse-Californie. Bulletin du Muséum d'Histoire Naturelle, Paris 4:371-384.
- Chace, F.A., Jr. 1962. The non-brachyuran decapod crustaceans of Clipperton Island. Proceedings of the United States National Museum 113(3416):605-635.
- Forest, J., and M. de Saint Laurent. 1968. Campagne de la "Calypso" au large des côtes Atlantiques de l'Amérique du sud (1961-1962). 6. Crustacés Décapodes: Pagurides. Annales de l'Institut Océanographique, Monaco, new series 45(2):47-172.
- Glassell, S.A. 1937. The Templeton Crocker Expedition. XI. Hermit crabs from the Gulf of California and west coast of Lower California. Zoologica 22: 241-263.
- Haig, J., T.S. Hopkins, and T.B. Scanland. 1970. The shallow water anomuran crab fauna of southwestern Baja California, Mexico. Transactions of the San Diego Society of Natural History 16:13-31.
- Harvey, A.W., and P.A. McLaughlin. 1990. Two new species of the *provenzanoi* group of *Pagurus* (Decapoda, Anomura, Paguridae) from the eastern Pacific with notes on their ecology. Contributions in Science, No. 425, pp. 13-21. Natural History Museum of Los Angeles County.
- Lemaitre, R., P.A. McLaughlin, and J. García-Gómez. 1982. The *Provenzanoi* group of hermit crabs (Crustacea, Decapoda, Paguridae) in the western Atlantic. Part IV. A review of the group, with notes on variations and abnormalities. Bulletin of Marine Science 32:670-701.
- McLaughlin, P.A. 1975. On the identity of *Pagurus brevidactylus* (Stimpson) (Decapoda: Paguridae), with the description of a new species of *Pagurus* from the western Atlantic. Bulletin of Marine Science 25: 359-376.
- Moran, D.A. 1984. Additions to the known anomuran fauna of El Salvador, Central America (Crustacea: Decapoda). Journal of Crustacean Biology 4:72-84.
- Nicolet, H. 1849. *Historia fisica y politica de Chile, Zoologia*, C. Gay, 3. Paris and Santiago. 547 pp.
- Rodriguez de la Cruz, M.C. 1987. Crustáceos decápodos del Golfo de California. Secretaria de Pesca, Mexico. 306 pp.
- Romero, C. 1982. Sistemática, biología y ecología de los anomuros (Crustacea Decapoda) de Laguna Percebu, Alto Golfo de California, BC., México. Tesis profesional, Univ. Autónoma de Baja California, Esc. de Ciencias Marinas. 207 pp.
- Romero, C., and A. Carvacho. 1988. Estudios ecológicos en Laguna Percebu, Alto Golfo de California. I. Crustáceos decápodos: anomuros sistemática ecología biogeografía y claves de identificación. [Ecological studies in Laguna Percebu, upper Gulf of California. I. Crustaceans (sic) decapods: Anomura systematics, ecology, biogeography and identification codes.] Ciencias Marinas 13:59-87.
- Snyder-Conn, E. 1980. Arthropoda: Crustacea Paguroidea and Coenobitoidea (hermit crabs). In *Common intertidal invertebrates of the Gulf of California*, R.

- C. Brusca, 275-285. University of Arizona Press, Tucson.
- Villalobos Hiriart, J.L., J.C.N. Rodriguez, A.C.D. Barriga, D.V. Martínez, P.F. Hernández, E.L. Fernández, and P.S. Valencia. 1989. Listados faunísticos de México. I. Crustáceos estomatopodos y decápodos intermareales de las islas del Golfo de California, México. Univ. Nacional Autónoma de México. i-ix + 114 pp.
- Von Prael, H. 1986. Crustáceos decápodos, asociados a diferentes habitats en la Ensenada de Utría, Chocó, Colombia. *Actualidades Biológicas* 15:95-99.
- Westervelt, C.A. 1967. The littoral anomuran decapod crustacean fauna of the Punta Peñasco-Bahía La Cholla area in Sonora, Mexico. Ph.D. Thesis, Univ. of Arizona, Tucson, 143 pp. *Dissertations Abstracts* 27B:4183-b.

Received 26 January 1990; accepted 19 June 1990.